PAOLO GUIDETTI

Laboratory of Zoology and Marine Biology, DiSTeBA, CoNISMa, University of Lecce, Italy
Tel: ++39(0)832-320853; e-mail: paolo.guidetti@unile.it

POPULATION DYNAMICS OF THE SEAGRASS *POSIDONIA OCEANICA* FOR EVALUATING MEADOW HEALTH STATUS: A STUDY CASE USING RECONSTRUCTION TECHNIQUES

RIASSUNTO

La dinamica di popolazione di tre praterie di *Posidonia oceanica* (L.) Delile in mar Ligure (Mediterraneo nord occidentale) è stata indagata attraverso metodi di ricostruzione al fine di ottenere indicazioni sugli effetti del ripascimento (BR) ed arricchimento organico (OE) rispetto a condizioni non disturbate (UN). Fasci foliari ortotropi sono stati campionati nel 1995: ad essi è stata attribuita l'età attraverso il conteggio di cicatrici e basi foliari che possono persistere sui rizomi di *P. oceanica* per decenni. Sono state così ottenute delle distribuzioni età-frequenza che riflettono il bilancio tra reclutamento e mortalità. Il tasso di formazione foliare è risultato più elevato presso BR, seguito da UN e OE, mentre l'intervallo plastocronico ha mostrato un 'pattern'inverso. Il reclutamento è risultato più elevato presso UN e OE rispetto a BR. I tassi di mortalità non sono risultati differenti tra le tre praterie. Nel complesso, *P. oceanica* è parsa essere in uno stato stazionario presso UN, in leggera espansione presso OE ed in declino presso BR, un quadro che fornisce l'evidenza di possibili effetti dei due tipi di disturbo indagati. Sebbene sia ovviamente necessario un appropriato piano di campionamento per trarre conclusioni circa lo stato di salute di *P. oceanica* su scala regionale, questi risultati suggeriscono che situazioni su scala locale possono influenzare le praterie di *P. oceanica* (con importanti implicazioni gestionali) al di là di fattori più generali che sono usualmente invocati per spiegare il declino delle fanerogame marine su ampia scala spaziale.

SUMMARY

Population dynamics of three *Posidonia oceanica* (L.) Delile meadows located along the coast of the Ligurian Sea (NW Mediterranean) were examined using reconstruction methods to provide evidence of the effects of beach replenishment (BR) and organic enrichment (OE) compared with an undisturbed condition (UN). Short orthotropic shoots were sampled in 1995: they were aged by counting scars

and leaf sheaths, which may persist along *P. oceanica* rhizomes for decades. Age-frequency distributions, reflecting the recruitment-mortality balance in seagrass populations, were thus constructed. The leaf formation rate was significantly highest at BR, followed by UN and OE meadows, whereas the plastochron interval showed an opposite pattern. Shoot recruitment was higher at UN and OE than at BR. Mortality rates did not statistically varied among meadows. *P. oceanica* hence appeared to be in approximate steady state at UN, slightly expanding at OE and declining at BR, a picture providing evidence of possible effects of the two impacts examined. Although a more appropriate sampling design should be necessary to support statements about the health status of *P. oceanica* on a regional scale, these results suggest that local point conditions might influence *P. oceanica* beds (with important management implications) besides more elusive general factors usually invoked to explain seagrass decline over a large spatial scale.

INTRODUCTION

The seagrass *Posidonia oceanica* (L.) Delile, endemic to the Mediterranean Sea, is a slow-growing species (DUARTE, 1991a) which forms widespread meadows from shallow areas to 40 m depth (OTT, 1980). This marine phanerogam dominates the Mediterranean infralittoral, contributing to a large percentage of the total primary production of the coastal zone (OTT, 1980) and providing habitats and resources to rich invertebrate and fish communities (MAZZELLA *et al.*, 1992; GUIDETTI, 2000a).
In the recent decades, many authors have identified several threats to the health of *P. oceanica* beds, which have undergone an evident decline in many regions of the Western Mediterranean (PÉRÈS and PICARD, 1975; BLANC and JEUDY DE GRISSAC, 1984; PEIRANO and BIANCHI, 1995; MARBÀ *et al.*, 1996; CAVAZZA *et al.*, 2000; GUIDETTI and FABIANO, 2000; GUIDETTI, 2001). However, the bulk of the available studies lack long-term data series; thus, baseline data are generally not available for monitoring programs. From this point of view, the use of reconstruction techniques (PERGENT *et al.*, 1989; DUARTE *et al.*, 1994; GUIDETTI, 2001) has been proposed as a useful tool to partially overcome the lack of previous data. These methods rely on the possibility to assign age to portions of seagrass rhizomes on the basis of the seasonal variability of a set of reiterative morphological modules (e.g., sheaths and internodes). They permit reconstruction of seagrass dynamics (e.g., leaf production rates) for a certain number of past years, to assign age to vertical shoots and, from this, to investigate shoot demography and population dynamics of seagrasses (see DUARTE *et al.*, 1994). The balance between shoot recruitment and mortality rates has thus been used by MARBÀ et al. (1996) as an indicator of the decline, the steady state or the expansion of *P. oceanica* populations along the Spanish coasts. Dating methods, anyway, are not fully accepted within the community of seagrass ecologists (see JENSEN *et al.*, 1996 and KALDY *et al.*, 1999). There are

nevertheless evidences indicating such methods as effective in providing useful information on seagrass dynamics and population status (DURAKO and DUARTE, 1997; but see also HEMMINGA and DUARTE, 2000). Recently, PETERSON and FOURQUREAN (2001) improved the model by DUARTE *et al.* (1994) (e.g., incorporating mortality of shoots aged <1 year in the gross mortality equations) and affirmed that, in spite of the necessary caution in data interpretation, there is no point to dismiss dating techniques for examining seagrass population dynamics.
The declining trend in *P. oceanica* meadows along the north-western coast of the Mediterranean Sea is well documented (MEINESZ *et al.*, 1991; PEIRANO and BIANCHI, 1995). In the Ligurian Sea, several authors (BALDUZZI *et al.*, 1984; BIANCHI and PEIRANO, 1995; PEIRANO and BIANCHI, 1995) related the decline of *P. oceanica* meadows with several sources of disturbance (e.g., alteration of the coastal sediment equilibrium, organic pollution, beach replenishment), but detailed studies that experimentally examined a cause-effect relationship still remain very scanty (GUIDETTI, 2001). This paper is aimed at investigating the effects of two sorts of point-source anthropogenic disturbances on the seagrass *P. oceanica* over a local scale.

MATERIALS AND METHODS

Samples were collected in 1995 from three *Posidonia oceanica* meadows located along the Ligurian coast (NW Mediterranean): Noli (8°25.2'E-44°12.6'N), Genoa-Quinto (9°0.7'E-44°23.1'N) and Prelo (9°13.6'E-44°20.2'N) (Fig. 1).

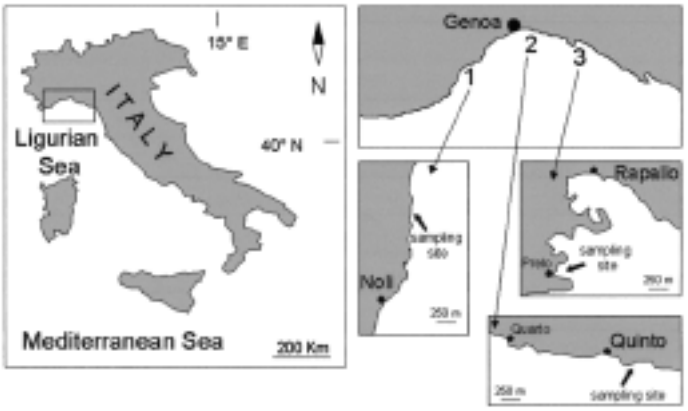

Fig. 1. - Sampling sites of *Posidonia oceanica:* 1) Noli (UN: undisturbed meadow); 2) Genoa-Quinto (OE: meadow impacted by sporadic organic loading); 3) Prelo (BR, meadow impacted by beach replenishments).

The Noli bed is located away from appreciable sources of anthropogenic disturbance so that it has been used as reference undisturbed meadow (hereafter named as

UN). The Genoa-Quinto meadow (named as OE), located off the eastern suburb of Genoa (approximately 700.000 inhabitants), is moderately exposed to nutrient enrichment being located nearby a biological water treatment plant sporadically discharging untreated waste waters. The effects of temporary organic loading and the main environmental characteristics of the marine waters (e.g., bacterial, chlorophyll a and nutrient concentrations, water temperature) at the studied site are reported in full by CARLI *et al.* (1992). The Prelo meadow (named as BR) was chiefly affected over the past years by beach replenishments, which caused decline in water clarity. Replenishment have often been made with inappropriate fine sediments. These latter were thus released from the beaches into the sea during the more intense winter storms and frequently resuspended by the wave action causing the formation of a wide belt of brownish waters along the shoreline. The increase in water turbidity in the marine area has been documented by GUIDETTI (2001) and demonstrated to decrease leaf production rates of *P. oceanica* in a meadow just adjacent to Prelo.

At the UN meadow, samples were taken at 6-7 m depth, where *P. oceanica* grows on coarse sand. Shoots from OE were collected at about 7-8 m depth on a coarse sandy bottom with sparse rocky formations, while, at BR, samples were taken at about 6 m depth where *P. oceanica* grows on sand and 'matte'. From 147 to 285 living orthotropic shoots (vertical growth) connected to 30-60 plagiotropic horizontal rhizomes were collected by removing clods within 5 quadrats (30 x 30 cm) randomly placed within each meadow. Samples were rinsed free of sediment carefully to avoid shoot breakage so that all shoots remained attached to the horizontal rhizomes. This prevented the problem usually faced by other authors about to include or not broken shoots in their analyses and the related bias (JENSEN *et al.,* 1997; PETERSON and FOURQUREAN, 2001).

To examine the age structure of living shoots, the following morphological measurements were conducted in the laboratory: number of shoots, number of standing leaves, number of sheaths and leaf scars per shoot, sheath thickness, length of internodes. The annual leaf formation rate (number of leaves produced per year) was estimated on the basis of the seasonal variability of plant modules, including the thickness of sheaths (leaf bases persisting along rhizomes after the leaf blade fall; PERGENT *et al.,* 1989) and the length of internodes (the distance between two adjacent scars left by sloughed leaves; DUARTE *et al.,* 1994; MARBÀ *et al.,* 1996). Both chronological signals (sheath thickness and the internodal length) were used complementarily in order to optimise the information collected according to GUIDETTI (2000b).

The knowledge of the average number of leaves produced annually per shoot in each of the three meadows allowed the calculation of the annual average leaf plastochron interval (PI, the time elapsed between the formation of 2 consecutive leaves; ERICKSON and MICHELLINI, 1957), and, in turn, translation of time in plastochron to absolute time (i.e., days or years).

The dynamics of *P. oceanica* populations was inferred from the age distribution of living shoots, from which estimates of shoot recruitment, shoot mortality and, consequently, net population growth rates were derived according to DUARTE *et al.* (1994) and MARBÀ *et al.* (1996). Shoot age was obtained by multiplying the total number of leaves produced by the shoot during its life-span (that is the sum of standing leaves plus leaf sheaths and scars = number of PIs) by the leaf PI.
The annual gross shoot recruitment rate (R_{gross} ln unit yr^{-1}) was calculated as:

$$R_{gross} = \ln \sum_{t=0}^{\infty} N_t - \ln \sum_{t=1}^{\infty} N_t$$

where $\sum_{t=0}^{\infty} N_t$ is the number of living shoots and $\sum_{t=1}^{\infty} N_t$ is the number of living shoots >1 yr.

Shoot mortality rate (M, ln units yr^{-1}) was obtained from the exponential decline of the number of living shoots (N_0) with time (t): $N_t = N_0 \cdot e^{-Mt}$, where N_0 is the number of shoots with an age equal to the mode, N_t is the number of shoots older than the modal age at time t, and M is the mortality rate (ln units in PI^{-1}).
The shoot mortality rate (M) was calculated using a semilogaritmic linear regression model, where mortality is considered to be constant over shoot age and years. Thus, the population half-life in years ($T_{1/2} = \ln 2/M$), which accounts for the time in which half of the recruited shoots will be dead, was used to provide a more intuitive description of the influence of shoot mortality on population turnover (DURAKO, 1994).
The ratio between recruitment and mortality (R:M) was used to distinguish between populations in expansion (R:M>1), in decline (R:M<1) or in steady state (R:M=1) (DUARTE and SAND-JENSEN, 1990; DUARTE *et al.*, 1994). Finally, the net rate of shoot population growth ($R_{net} = R_{gross} - M$; DUARTE *et al.*, 1994) was used to forecast the future development of the meadows studied.
Analysis of variance (One Way ANOVA) was used to compare means of some variables (e.g., shoot density, leaf formation rate) among the three *P. oceanica* populations studied. Before analysis, all data to be analysed by parametric ANOVAs were tested by Cochran test for homogeneity of variances. Whenever necessary, they were appropriately transformed and newly tested. Post-hoc differences were tested by SNK test (UNDERWOOD, 1997). Differences in the median shoot age among meadows, due to the non-normal distribution of data, were tested by the non-parametric Kruskall-Wallis test (ANOVA on ranks). Dunn's method was employed for multiple comparisons a "posteriori" since treatment group sizes were unequal (SOKAL and ROHLF, 1981).

RESULTS

The shoot density of *Posidonia oceanica* did not show any statistically significant difference among the three meadows examined (Table 1; ANOVA: F=1.62, p=0.22). The leaf formation rate was significantly highest at BR, followed by UN and, in turn, OE (ANOVA: F=92.12; p<0.001; SNK test: p<0.05), while leaf plastochron interval showed an opposite pattern (Table 1). The maximum shoot age was observed at the OE bed, followed by UN and BR (Table 1). The difference in the median shoot age among meadows (Table 1) was statistically significant (Kruskall-Wallis test: H=35.5, p<0.001). Dunn's method revealed that the median shoot age calculated at BR was significantly lower than those from the OE and UN beds (Q=5.6 and Q=3.9, respectively; p<0.05), whereas no difference was observed between UN and OE (Dunn's test: Q=1.4). The age structure of *P. oceanica* shoots displayed a mode of shoots between 1 and 4 years old and an exponential decline in shoot abundance with increasing age due to mortality in particular at BR (Table 1, Fig. 2). The differences in the modal age indicate a severe reduction in shoot recruitment over the few preceding years. Recruitment, in fact, appeared to decrease over the past few

	Population		
Variable	UN	OE	BR
Shoot density (no. shoots m^{-2})	433.1 ± 48.7	460.0 ± 38.8	513.3 ± 48.0
Leaf formation rate (no. leaves sh^{-1} yr^{-1})	6.52 ± 0.43	6.23 ± 0.39	7.31 ± 0.35
Plastochron interval (days)	56.0	58.6	49.9
Maximum shoot age (yr)	23	35	16
Median shoot age (yr)	7	11.5	5
Shoot recruitment rate (ln units yr^{-1})	0.12	0.14	0.02
Shoot mortality rate (ln units yr^{-1})	0.09 ± 0.02	0.06 ± 0.02	0.11 ± 0.04
Population half-life (yr)	7.7	11.6	6.3
Net recruitment rate (ln units yr-1)	0.03	0.08	-0.09
State of the meadows	steady	expanding	declining

TABLE 1. – Shoot density, leaf formation rate, plastochron interval, and main variables related to demographics of *P. oceanica* (mean values ± SE) in the three meadows studied (UN: Noli, undisturbed meadow; OE: Genoa-Quinto, meadow impacted by sporadic organic loading; BR: Prelo, meadow impacted by beach replenishments).

years mainly at the BR meadow (Fig. 2). Shoot recruitment rate was thus similar at UN and OE, whereas the significantly lowest value was estimated at BR (ANOVA: F=3.74, p=0.02; SNK test: p<0.05; Table 2). In contrast, shoot mortality rate did not vary significantly among beds (ANOVA: F=0.49, p=0.62; Table 1). Population half-life was high at OE in comparison with UN and BR meadows (Table 1).
The calculated net rate of population change (R_{gross}–M) predicted different fates for the three meadows investigated (Table 1). The UN meadow was in approximate

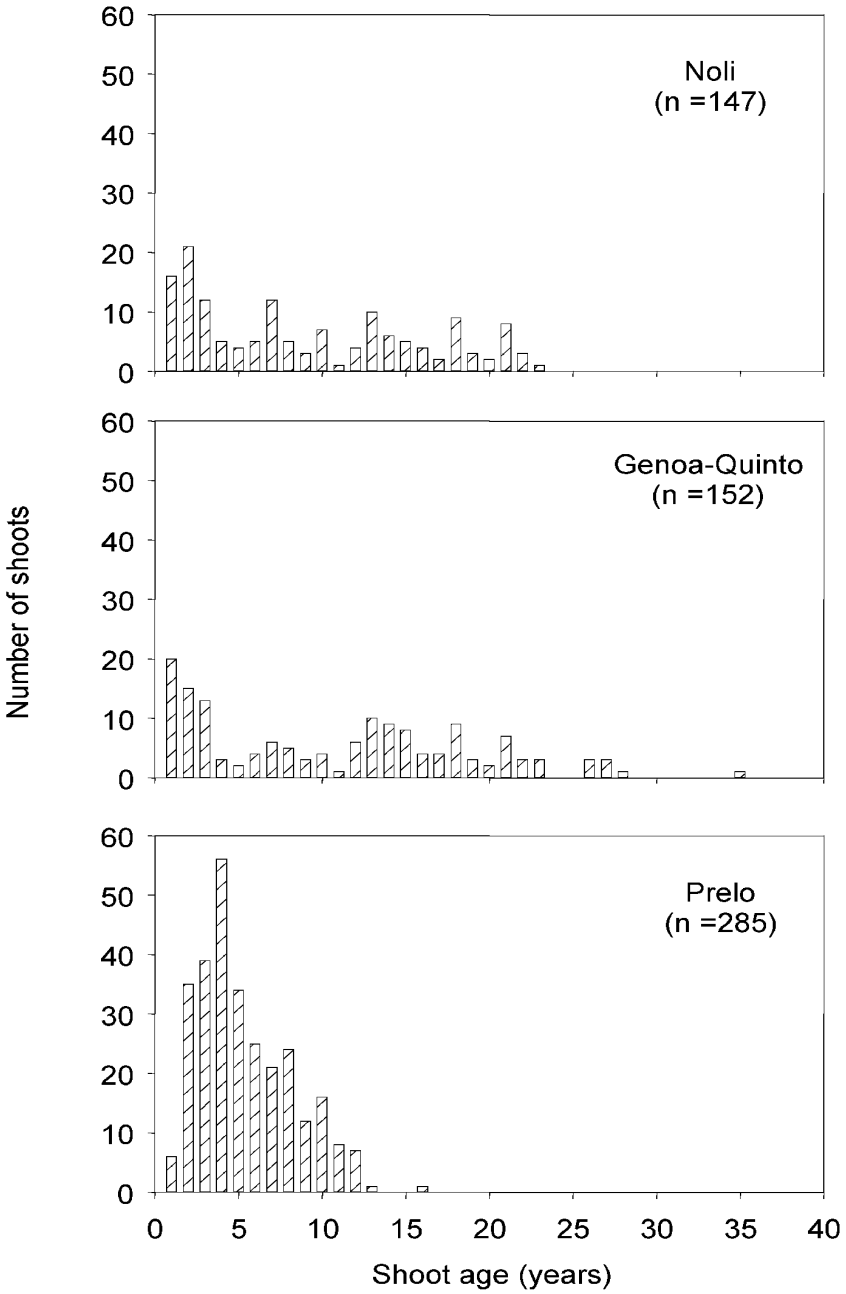

Fig. 2. - Age structure of living orthotropic shoots of *Posidonia oceanica* from each of the three populations studied (UN: Noli, undisturbed meadow; OE: Genoa-Quinto, meadow impacted by sporadic organic loading; BR: Prelo, meadow impacted by beach replenishments).

steady state, the OE *P. oceanica* bed appeared to be slightly expanding and the BR meadow seemed to undergo decline.

DISCUSSION

In the past several decades, seagrass decline has been reported from several areas of the world (ORTH and MOORE, 1983; CAMBRIDGE and McCOMB, 1984; MEINESZ *et al.*, 1991; SHORT and ECHEVERRIA, 1996; PULICH and WHITE, 1991; ROBBLEE *et al.*, 1991; MARBÀ *et al*., 1996) with implications of the dramatic loss of these important habitats. Seagrass meadows have been usually monitored by examining yearly changes in seagrass coverage, shoot density and in dynamic features, such as leaf production (ROBBINS and BELL, 1994; PERGENT *et al.*, 1995; PERGENT-MARTINI and PERGENT, 1996; GUIDETTI and FABIANO, 2000; GUIDETTI, 2001). In recent years, several authors (DUARTE *et al.*, 1994; PERGENT *et al.*, 1995; MARBÀ *et. al.* 1996; GUIDETTI and FABIANO, 2000) have emphasised the usefulness and suitability of reconstructive dating methods as powerful tools able to provide information on past events of environmental disturbance in areas colonised by the seagrass *P. oceanica*. These techniques, in fact, allow a fast evaluation of leaf production and rhizome growth rates and their changes over time. Even more with regard to the leaf production of *P. oceanica,* such methods appear to be more suitable in monitoring programmes focused on the assessment of interannual variations in comparison with other classical approaches, such as leaf marking, measurements of oxygen and of ^{14}C assimilation, and indirect estimates of seagrass production derived by measurements of environmental variables related to photosynthesis (see GUIDETTI *et al.,* 2000, and GUIDETTI and FABIANO, 2000).

Reconstruction methods have also been used to examine shoot population dynamics and to forecast the development of seagrass populations, chiefly for long-living species, in several areas of the world (DURAKO, 1994; GALLEGOS *et al.*, 1994; DUARTE *et al.*, 1994; MARBÀ *et al.*, 1996; MARBÀ and WALKER, 1999). However, some authors have recently argued that the required assumptions of constant age-specific mortality and recruitment rate are untenable, and that PI durations are highly variable in space and time due to the environmental influences (JENSEN *et al.*, 1996). In addition, KALDY *et al.* (1999), after reiterating these concerns, discouraged the use of dating methods for construction of age-frequency distributions of *Thalassia testudinum* because the assumption of equal elapsed time between successive leaf formation was violated. They also affirmed that the assumption that internode length patterns imprinted on vertical rhizomes represent annual cycles must still be tested and that sexual reproductive events may alter resource allocation thus affecting leaf and rhizome growth rates. Recently PETER-

SON and FOURQUREAN (2001) carried out a large-scale investigation on seagrass (*Thalassia testudinum*) demographics in south Florida (USA) and raised several points about the use of dating methods. They improved the previous model by DUARTE *et al.* (1994) and advised authors about how to proceed in future studies (e.g., using site-specific leaf production rates). The conclusion of these latter authors was that dating methods (and related models of seagrass demography to forecast future developments) need further improvements and experimentation for reducing the present level of uncertainty and testing assumptions. However, such studies may enable seagrass ecologists to collect information to identify areas of management concern or to frame questions that address the controlling mechanisms influencing population growth, in spite of the necessary caution for data interpretation.

In the light of the above issues and considering the specific case of *P. oceanica,* there is some point that has to be raised. First, sexual reproduction in *P. oceanica* is a fairly rare event, even more in the north-western sector of the basin (BOUDOURESQUE and THELIN, 1985), so that the influence of such an event on the leaf and rhizome production rates may be considered less important. Furthermore, the annual cycle in the sheath morphology of *P. oceanica* has been widely demonstrated (PERGENT *et al.*, 1989; PERGENT 1990; PERGENT-MARTINI *et al.*, 1994) and the estimates of the PI deriving from counting sheaths is subject to a smaller error than using scars only (see GUIDETTI, 2000b). Leaf production rate obtained by counting sheaths is, in practice, an yearly average leaf production rate, whose use has been strongly advised by PETERSON and FOURQUREAN (2001) to avoid bias potentially associated to seasonality. Again, PETERSON and FOURQUREAN (2001) found that PI was highly variable over space and strongly suggested the use of site-specific leaf production rates (i.e, the inverse of PI) which is just what has been done estimating PI for each of the three *P. oceanica* beds.

With regard to the results presented here, shoot density among the three meadows investigated did not change in spite of the different environmental conditions they were experiencing. The values measured at the three sites substantially fall in the 'normal density' ranges, according to PERGENT *et al.* (1995). In this case, therefore, shoot density did not respond to the levels and sorts of disturbances studied. As regards demographics, these data are comparable with those reported by MARBÀ *et al.* (1996) for Spanish Mediterranean coasts. It is worth noting the high maximum shoot age found at Genoa-Quinto compared with the values reported by MARBÀ *et al.* (1996), while median ages are similar. In spite of the variability in the absolute values of gross recruitment and mortality rates when related to the predicted development of the meadows, the resultant net recruitment rates (which account for the balance between gross recruitment and mortality) reported by MARBÀ *et al.* (1996) are similar with the values from the Ligurian Sea.

The results obtained about the three *P. oceanica* meadows in the Ligurian Sea, on the whole, provide suggestive evidence of the possible effects of different distur-

bances on *P. oceanica* demography and are fairly consistent with the literature information. On the basis of these results, the *P. oceanica* bed at Noli was in a steady state, which agrees with the absence of severe sources of disturbance. The meadow is reported to extend between the surface and about 20 m depth, without evident discontinuities (e.g., erosion channels), except east-wards where regression is mainly attributed to the mechanical effects of fishing gears (BIANCHI and PEIRANO, 1995). The Genoa-Quinto meadow appeared to be slightly expanding. At this location, *P. oceanica* is reported to extend from about 6 to 30 m depth, which represents a comparatively wide bathymetric range for *P. oceanica* (BALDUZZI *et al.*, 1984; DUARTE, 1991b; BIANCHI and PEIRANO, 1995). The presence of the treatment plant and the sporadic nature of untreated waste water inputs, therefore, do not negatively affect *P. oceanica,* differently from the impact of heavy nutrient enrichment observed elsewhere (see for instance PERGENT-MARTINI and PERGENT, 1996). This meadow thus displays a good health status, as also confirmed by previous studies (BALDUZZI *et al.,* 1984; BIANCHI and PEIRANO, 1995), except in the area immediately surrounding the outlet (BALDUZZI *et al.*, 1984). As far as the Prelo meadow is concerned, BIANCHI and PEIRANO (1995) reported that *P. oceanica* extends homogeneously at shallow depth and that the meadow ends at about 9-10 m depth with an eroded margin. The presence of dead 'matte'is reported at greater depths, which testifies the regression of the lower limit. In some areas, evident signs of damages due to anchoring have been observed (pers. obs.), while in others *P. oceanica* shoots have undergone burial (BALDUZZI *et al.,* 1984). Being subject to an intense tourism pressure since the last decades, the general decline of this meadow is likely to be chiefly attributed to the alteration of the sediment dynamics following the construction of jetties and artificial beaches replenished by non-appropriate materials. From this point of view, GUIDETTI (2001) recently detected the decrease in leaf production rate following a single replenishment in a meadow next to Prelo.

The same author roughly estimated that about 3 years are necessary for a complete recovery after a single intervention. All the above issues support the statements by MEINESZ *et al.* (1991) and MARBÀ et al. (1996), who associated the demise of some *P. oceanica* populations along the French and Spanish Mediterranean coasts, respectively, with burial or erosion derived from construction works along the coast and the increasing beach frequentation. Furthermore, GUIDETTI and FABIANO (2000) demonstrated the decline of the leaf primary production of *P. oceanica* following human-induced increase in water turbidity at Ischia island (Gulf of Naples, Italy).

Results suggest that, in spite of the general declining trend of *P. oceanica* meadows, local sources of human disturbances may affect *P. oceanica* meadows. However, to have a thorough assessment of the health status of *P. oceanica* on a regional scale it is necessary to extend this investigation to a higher number of meadows and to implement appropriate sampling designs in order to separate the effects of more elu-

sive non-point source disturbances which may superimpose on local causes in impacting *P. oceanica* populations.

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REFERENCES

BALDUZZI A., BAVASTRELLO G., BELLONI S., BOERO F., CATTANEO R., PANSINI M., PRONZATO R., 1984 - *Valutazione dello stato di alcune praterie di Posidonia del mare Ligure sottoposte a diverse condizioni di inquinamento.* In: C.F. BOUDOURESQUE, A. JEUDY DE GRISSAC and J. OLIVIER (eds.), International Workshop on *Posidonia oceanica* Beds. GIS Posidonie Publ.: 73-78.

BIANCHI C. N., PEIRANO A., 1995 - *Atlante delle Fanerogame Marine della Liguria: Posidonia oceanica and Cymodocea nodosa.* ENEA, Centro Ricerche Ambiente Marino, ENEA-CRAM, La Spezia, Italia.

BLANC J. J., JEUDY DE GRISSAC A., 1984 - *Érosion sous-marines des herbiers à Posidonia oceanica (Méditerranée).* In: C.F. BOUDOURESQUE, A. JEUDY DE GRISSAC AND J. OLIVIER (eds.), International Workshop on *Posidonia oceanica* Beds. GIS Posidonie Publ.: 23-28.

BOUDOURESQUE C. F., THELIN I., 1985 - *Floraison et fructification de Posidonia oceanica: un protocole d'étude standardisé.* Rapp. Comm. int. Mer Médit., 29: 177-179.

CAMBRIDGE M. L., MCCOMB A.J., 1984 - *The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in rela - tion to industrial development.* Aquat. Bot., 20: 229-243.

CARLI A., BANDELLONI R., MARIOTTINI G. L., PANE L., PRUZZO C., ROMAIRONE V., 1992 - *The plankton biotic community and eutrophication in coastal areas of the Gulf of Genoa.* In: R. A. VOLLENWEIDER, R. MARCHETTI AND R. VIVIANI (eds.), *Marine Coastal Eutrophication.* Sci. Total Environ. (suppl.): 693-696.

CAVAZZA W., IMMORDINO F., MORETTI L., PEIRANO A., PIRONI A., RUGGIERO F., 2000 - *Sedimentological parameters and seagrass distribution as indicators of anth - ropogenic coastal degradation at Monterosso Bay (Ligurian Sea, NW Italy).* J. Coast. Res., 16: 295-305.

DUARTE C. M., SAND-JENSEN K., 1990 - *Seagrass colonisation: biomass develop - ment and shoot demography in Cymodocea nodosa patches.* Mar. Ecol. Prog. Ser., 67: 97-103.

DUARTE C. M., 1991a - *Allometric scaling of seagrass form and productivity.* Mar. Ecol. Prog. Ser., 77: 298-300.

DUARTE C. M., 1991b - *Seagrass depth limits.* Aquat. Bot., 40: 363-377.

DUARTE C. M., MARBÀ N., AGAWIN N., CEBRIÀN J., ENRIQUEZ S., FORTES M. D., GALLEGOS M.E., MERINO M., OLESEN B., SAND-JENSEN K., URI J., VERMAAT J., 1994 - *Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist.* Mar. Ecol. Prog. Ser., 107: 195-209.

DURAKO M. J., 1994 - *Seagrass die-off in Florida Bay (USA): changes in shoot demographic characteristics and population dynamics in Thalassia testudinum.* Mar. Ecol. Prog. Ser., 110: 59-66.

DURAKO M. J., DUARTE C. M., 1997 - *On the use of reconstructive aging techniques for assessing seagrass demography: a critique of the model test of Jensen et al.* (1996). Mar. Ecol. Prog. Ser., 146: 297-303.

ERICKSON R. O., MICHELLINI F. J., 1957 - *The plastochron index.* Am. J. Bot., 44: 297-305.

GALLEGOS M. E., MERINO M., RODRIGUEZ A., MARBÀ N., DUARTE C. M., 1994 - *Growth patterns and demography of pioneer Caribbean seagrasses Halodule wrightii and Syringodium filiforme.* Mar. Ecol. Prog. Ser., 109: 99-104.

GUIDETTI P., 2000a - *Differences among fish assemblages associated with nearsho - re Posidonia oceanica seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea.* Estuar. Coast. Shelf Sci., 50: 515-529.

GUIDETTI P. 2000b - *Leaf primary production in Posidonia oceanica: two recon - structive aging techniques give similar results.* Aquat. Bot., 68: 337-343.

GUIDETTI P., 2001 - *Detecting environmental impacts on the Mediterranean sea - grass Posidonia oceanica (L.) Delile: the use of reconstructive methods in com - bination with 'beyond BACI' designs.* J. Exp. Mar. Biol. Ecol., 260: 27-39.

GUIDETTI P., BUIA M. C., MAZZELLA L., 2000 - *The use of lepidochronology as a tool of analysis of dynamic features in the seagrass Posidonia oceanica of the Adriatic Sea.* Bot. Mar., 43: 1-9.

GUIDETTI P., FABIANO M., 2000 - *The use of lepidochronology to assess the impact of terrigenous discharges on the primary leaf production of the Mediterranean seagrass Posidonia oceanica.* Mar. Poll. Bull., 40: 449-453.

HEMMINGA M., DUARTE C. M., 2000 - *Seagrass Biology.* University Press, Cambridge.

JENSEN S. L., ROBBINS B. D., BELL S. S., 1996 - *Predicting population decline: sea - grass demographics and the reconstructive techniques.* Mar. Ecol. Prog. Ser., 136: 267-276.

KALDY J. E., FOWLER N., DUNTON K. H., 1999 - *Critical assessment of Thalassia testudinum (turtle grass) aging techniques: implications for demographic infe - rences.* Mar. Ecol. Prog. Ser., 181: 279-288.

MARBÀ N., DUARTE C. M., CEBRIAN J., GALLEGOS M. E., OLESEN B., SAND-JENSEN K., 1996 - *Growth and population dynamics of Posidonia oceanica on the Spanish Mediterranean coast: elucidating seagrass decline.* Mar. Ecol. Prog. Ser., 137: 203-213.

MARBÀ N., WALKER D. I., 1999 - *Growth, flowering, and population dynamics of temperate Western Australian seagrasses.* Mar. Ecol. Prog. Ser., 184: 105-118.

MAZZELLA L., BUIA M. C., GAMBI M. C., LORENTI M., RUSSO G. F., SCIPIONE M. B., ZUPO V., 1992 - *Plant-animal trophic relationships in the Posidonia oceanica ecosystem of the Mediterranean Sea: a review.* In: D. M. JOHN, S. J. HAWKINS AND J.H. PRICE(eds.), *Plant-Animal Interactions in the Marine Benthos.* The Systematic Association vol 46. Claredon Press, Oxford: 165-187 pp.

MEINESZ A., LEFEVRE J. R., ASTIER J. M., 1991 - *Impact of coastal development on the infralittoral zone along the southern Mediterranean shore of continental France.* Mar. Poll. Bull., 23: 343-347.

ORTH R. J., MOORE K. A., 1983 - *Chesapeake Bay: an unprecedented decline in sub - merged aquatic vegetation.* Science, 222: 51-53.

OTT J., 1980 - *Growth and production in Posidonia oceanica (L.) Delile.* P.S.Z.N. I: Mar. Ecol., 1: 47-64.

PEIRANO A., Bianchi C. N., 1995 - *Decline of the seagrass Posidonia oceanica in response to environmental disturbance: a simulation-like approach off Liguria (NW Mediterranean Sea). Proceedings of the 30th E.M.B.S.*, Southampton, U.K., September 1995: 87-95.

PÉRÈS J. M., PICARD J., 1975 - *Causes de la rarefaction et de la disparition des her - biers de Posidonia oceanica sur les côtes françaises de la Méditerranée.* Aquat. Bot., 1: 133-139.

PERGENT G., BOUDOURESQUE C.F., CROUZET A., MEINESZ A., 1989 - *Cyclic changes along Posidonia oceanica rhizomes (lepidochronology): present state and per - spectives.* P.S.Z.N.: Mar. Ecol., 10: 221-230.

PERGENT G., 1990 - *Lepidochronological analysis of the seagrass Posidonia ocea - nica (L.)* Delile: a standardised approach. Aquat. Bot., 37: 39-54.

PERGENT G., PERGENT-MARTINI C., BOUDOURESQUE C. F., 1995 - *Utilisation de l'herbier a Posidonia oceanica comme indicateur biologique de la qualité du milieu littoral en Méditerranée: état des connaissances.* Mesogée, 54: 3-27.

PERGENT-MARTINI C., PERGENT G., 1996 - *Spatio-temporal dynamics of Posidonia oceanica beds near a sewage outfall (Mediterranean-France).* In: J. KUO, R.C. PHILLIPS, D. I. WALKER AND H. KIRKMAN (eds.), *Proceeding of an International Workshop*, Rottnest Island, Western Australia: 299-306.

PERGENT-MARTINI C., RICO-RAIMONDINO V., PERGENT G., 1994 - *Primary production of Posidonia oceanica in the Mediterranean basin.* Mar. Biol., 120: 9-15.

PETERSON B. J., FOURQUREAN J. W., 2001 - *Large-scale patterns is seagrass (Thalassia testudinum) demographics in south Florida.* Limnol. Oceanogr., 46: 1077-1090.

PULICH W. M., WHITE W. A., 1991 - *Decline of submerged vegetation in the Galveston Bay system: chronology and relationships to physical processes.* J. Coast. Res., 7: 1125-1138.

ROBBINS B. D., BELL S. S., 1994 - *Seagrass landscapes: a terrestrial approach to the marine subtidal environment.* Trends Ecol. Evol., 9: 301-304.

ROBBLEE M. B., BARBER T. R., CARLSON P. R. JR, DURAKO M. J., FOURQUREAU J. W., MUEHLSTEIN L. K., PORTER D., YARBRO L. A., ZIEMAN R. T., ZIEMAN J. C., 1991 - *Mass mortality of the tropical seagrass Thalassia testudinum in Florida Bay (USA).* Mar. Ecol. Prog. Ser., 71: 297-299.

SHORT F. T., WYLLIE-ECHEVERRIA S., 1996 - N*atural and human-induced distur - bance of seagrasses.* Environ. Conserv., 23: 17-27.

SOKAL R. R., ROHLF F. J., 1981 - *Biometry*, 2nd ed. *The Principles and Practice of Statistics in Biological Research.* Freeman and Co., New York.

UNDERWOOD A. J., 1997 - *Experiments in Ecology: Their Logical Design and Interpretation using Analysis of Variance.* Cambridge University Press, Cambridge.